Z. Säugetierkunde 56 (1991) 1–9

ISSN 0044-3468

A parapatric scenery: the distribution and ecology of *Sorex araneus* and *S. coronatus* (Insectivora, Soricidae) in southwestern Germany

By H. Brünner and C. R. Neet

Institut für Biologie I (Zoologie), Universität Freiburg, FRG, and Institut de Zoologie et d'Ecologie Animale, Université de Lausanne, Switzerland

Receipt of Ms. 7. 6. 1990
Acceptance of Ms. 31. 7. 1990

Abstract

Studied the distribution of *Sorex araneus* and *S. coronatus* in southwestern Germany along a transect from the Upper Rhine Valley to the highest elevation, the Feldberg, in the Black Forest. The species were determined by polyacrylamide gel electrophoresis of total blood proteins. In the study area, the two species occurred in parapatry and showed an alternating altitude distributional pattern.

S. araneus was found in the bottom of the Upper Rhine Valley and in the heights of the Feldberg, while *S. coronatus* was present in the lower and intermediate altitude levels of the Black Forest. In the Zastler Valley, *S. coronatus* advances 400 m farther uphill than in the St. Wilhelmer Valley where the climate is relatively cold and inclement. Two contact zones were found, situated at different altitudes according to the valley. In the study area, the species appeared to be altitudinal vicariads.

The ecology and distributional history of *S. araneus* and *S. coronatus* are discussed in comparison with available data on their respective areas of distribution. It is argued that *S. araneus* occupies regions with rather continental climatic characters either on dry or wet soils. On the other hand, *S. coronatus* prefers Atlantic climates and balanced soil humidity. The competitive interaction between *S. coronatus* and *S. araneus* and its biogeographical consequences are discussed.

Introduction

During the last 40 years, it gradually became obvious that in central and western Europe, the taxon *Sorex araneus* included a second, cryptic species: *Sorex coronatus* (e.g. Hausser et al. 1985; Neet 1989a; Hausser 1990; Hausser et al. 1990). The two species are actually defined by their karyotypes (Meylan and Hausser 1978) and have been shown to be clearcut species that do not hybridize (Neet and Hausser 1989).

Since the first records of *S. coronatus* in Germany (Olert 1973; Schwammberger 1976), some information has been published on its distribution in the Rhineland and Westphalia by Handwerk (1987). However, only very few data are available for southern Germany (Brünner and Hoffrichter 1987; Braun and Kischnick 1987; Knoch 1989).

In this paper we present new information on the distribution and ecology of *S. araneus* and *S. coronatus* in southwestern Germany (Freiburg region) and discuss their parapatric distribution in Europe, making special reference to the comparison of the distribution of the two species in southwestern Germany and western Switzerland.

Material and methods

Shrews have been trapped in the dense, herbaceous vegetation found along small rivers or in similar vegetation along woodland paths. The trapping sites lie on a transect from the Kaiserstuhl in the Upper Rhine Valley to the Feldberg in the Black Forest. 100 live traps (Sherman, Tallahassee, USA) baited with a mixture of sardines in oil and rolled oats were exposed during 23 trapping dates in 19 trapping sites. A total amount of 87 shrews was captured and determined biochemically.

For electrophoretic determination, a blood sample of about 2 µl was taken from the tail. Blood samples were diluted in a buffer solution, analysed according to a standard technique (Hausser and Zuber 1983) and identified by the characteristic albumin patterns (Neet and Hausser 1989). As the electrophoretic technique has been tested in Switzerland only, karyological analyses were undertaken with some of the specimens of *S. araneus* and *S. coronatus* in order to ascertain the reliability of the electrophoretic method in southwestern Germany (see Neet 1989a, for a discussion of the limitations of the applicability of the technique).

Karyotypes were prepared in the laboratory from air dried mitotic chromosomes taken from bone marrow cells. The preparations were either Giemsa stained in a 4 % solution (Baker et al. 1982) or G-banded (Seabright 1971). All the *S. araneus* specimens analysed from southwestern Germany belonged to the "Vaud" karyotype with 22–24 (NF = 40) meta- and acrocentric autosomes, i.e. the same karyotype as the one used to test the biochemical determination techniques (Neet 1989a; Neet and Hausser 1989). The individuals of *S. coronatus* all had 20 metacentric autosomes (NF = 44).

Results

In the study area, *S. araneus* and *S. coronatus* appear to be parapatrically distributed, i.e. in conjunct contact, without wide zones of sympatry (Fig. 1). The corresponding list of trapping sites includes the altitudes at which the two species were caught (Table 1).

Only one species, *S. araneus*, was found in the Upper Rhine Valley near Freiburg (Mooswald) and on the Kaiserstuhl. On the lower slopes of the Black Forest (near Ehrenkirchen) and of the Zartener Becken (near Freiburg), *S. coronatus* was the only species to be captured. In the Feldberg region, *S. coronatus* was the only species found up to 730 m in the Zastler Valley, and up to 700 m in the Bruggatal and in the St. Wilhelmer Valley. The upper limit of distribution of *S. coronatus* is at about 1050 m in the Zastler Valley and 700 m in the St. Wilhelmer Valley. *S. araneus* is found between 900 m and 1450 m in the Zastler Valley and between 790 m and up to the top at the Feldberg (1496 m) in the St. Wilhelmer Valley.

As one would expect according to this altitudinal segregation pattern where *S. araneus* is found in the lowlands and higher mountain altitudes, while *S. coronatus* inhabits middle range altitudes, two contact zones were found. In these zones, as in other contact zones studied in Switzerland (Neet and Hausser 1990), the two species may coexist. The first contact zone is situated in the middle of the Zastler Valley, at 900 m, and the second one on the Schönberg, a foothill of the Black forest, at 400 m.

Discussion

Distribution of *S. araneus* and *S. coronatus* in southwestern Europe

The results presented here strongly suggest a parapatric distribution of the two species in southwestern Germany. This is consistent with the general pattern described in central and western Europe by Hausser et al. (1985). The alternating altitude distribution found here also corresponds to the one found in western Switzerland (Hausser 1978) and confirms current views on the ecology of the two species.

As a matter of fact, *S. coronatus* inhabits wide areas of northwestern Spain and most parts of France. In these countries, *S. araneus* is restricted to higher altitudes (Pyrénées, Massif central, Alpes), and the parapatric distribution is clearcut (Hausser et al. 1985).

Moving towards the east and the north of Europe, the parapatrical distribution turns out to be progressively realized on a meso-distributional level and becomes more and more difficult to visualize on a large scale. In Switzerland, *S. coronatus* is mainly present in the lowlands, the lower parts of the Jura and the Alps. In some places this species may, however, extend up to 1400 m of altitude. *S. araneus* is the dominant species above 800 m, but also occurs at low altitudes in wet habitats such as the borders of the Lake of Neuchâtel. Although a simple histogram of their altitudinal distributions suggests a wide

zone of sympatry, all detailed distributional studies have confirmed strict parapatry with contact zones never exceeding a few hundred meters (Hausser 1978; Hausser and Bourquin 1988; Neet 1989a; Neet and Hausser 1990). In Belgium, *S. coronatus* is the most common species in the western parts of the country. *S. araneus* appears in the eastern lowlands and the medium altitudes in the south of the country (Mys et al. 1985). In Holland, *S. araneus* occurs alone in the depressions in the north but the two species are believed to co-occur in the remainder of the country (Loch 1977). There is, however, some evidence that *S. araneus* is mainly distributed in areas below sea level, while *S. coronatus* occurs in areas above this level (Hausser pers. comm.). In northeastern Germany the two species co-occur over a large area: Niederrheinische Tiefebene, Mittelrhein, westfälische Bucht, Rheinisches Schiefergebirge (Hutterer and Vierhaus 1984; Handwerk 1987).

One can sum up at this point by stating that *S. coronatus* is found in areas with a balanced Atlantic climate, while *S. araneus* occurs in colder or wetter habitats, and that the parapatric distribution is decreasingly distinct as one proceeds towards the north of Europe.

Distributional ecology of *S. araneus* and *S. coronatus* in southwestern Germany

In southern Germany three climatic zones have been differentiated (Liehl and Sick 1984): 1. the warm, dry and continental Upper Rhine Valley; 2. the humid lower-altitude foothills of the Black Forest (up to 600 m), with an Atlantic climate; and 3. the heights of the Black Forest (up to 1500 m) with a typically subalpine climate and abundant rainfall. These zones closely correspond to the altitudinal distribution zones of the two species *S. araneus* and *S. coronatus*. The first species is found in the Upper Rhine Valley and above 790 m in the Black Forest, while the second is mainly found at low altitudes of the Black Forest. Interestingly, a correspondance between altitudinal zones of vegetation and the distribution of the two species has also been demonstrated in western Switzerland (Neet 1989a).

The glacier-formed St. Wilhelmer Valley is wide with high nocturnal eradiation. It opens with a gradual slope into the Bruggatal almost right angles at a very narrow point (Fig. 1). Thus, the cold air is often congested providing a rough climate. Moreover, the valley is on a lee position with rather low rainfall. In contrast, the Zastler Valley is narrow and steep sloping with several steps. It describes a slight bow and opens widely into the Bruggatal (Fig. 1). Thus, the cold air from the Feldberg heights can discharge quickly without any obstacle. As it is in a windward position, higher rainfall is noted (Schwabe-Kratochwil and Bogenrieder, pers. comm.). In the St. Wilhelmer Valley, *S. coronatus* was trapped up to an altitude of 700 m, in contrast to the climatically favoured Zastler Valley, where it can be found up to 1050 m.

An interesting parallelism with this observation has been reported for a contact zone of the *Sorex* species in a valley of the Valaisan Alps between Val d'Illiez and Champéry (Meylan 1964; Ott 1968). There, *S. coronatus* occurred on the southeastern slopes of the valley about 1 km farther uphill than on the other side of the river at the bottom of the northwestern slopes. It can be supposed that the banks along the southeastern slopes are also climatically favoured, thus enabling *S. coronatus* to reach higher into the Valley. Other similar examples have been found for the distribution of the two species in Switzerland (Hausser and Bourquin 1988).

Another distributional pattern, similar to the one found in our study area, can be expected to be found for the two *Sorex* species in northern Baden, where *S. araneus* was trapped in the Hardt Forest near Karlsruhe (Brünner unpub.) and in several locations in the south of Rastatt (Niethammer pers. comm.). *S. coronatus* was found in a beech forest at 300 m on the western slopes of the Black Forest. In this area, 26 individuals of *S.*

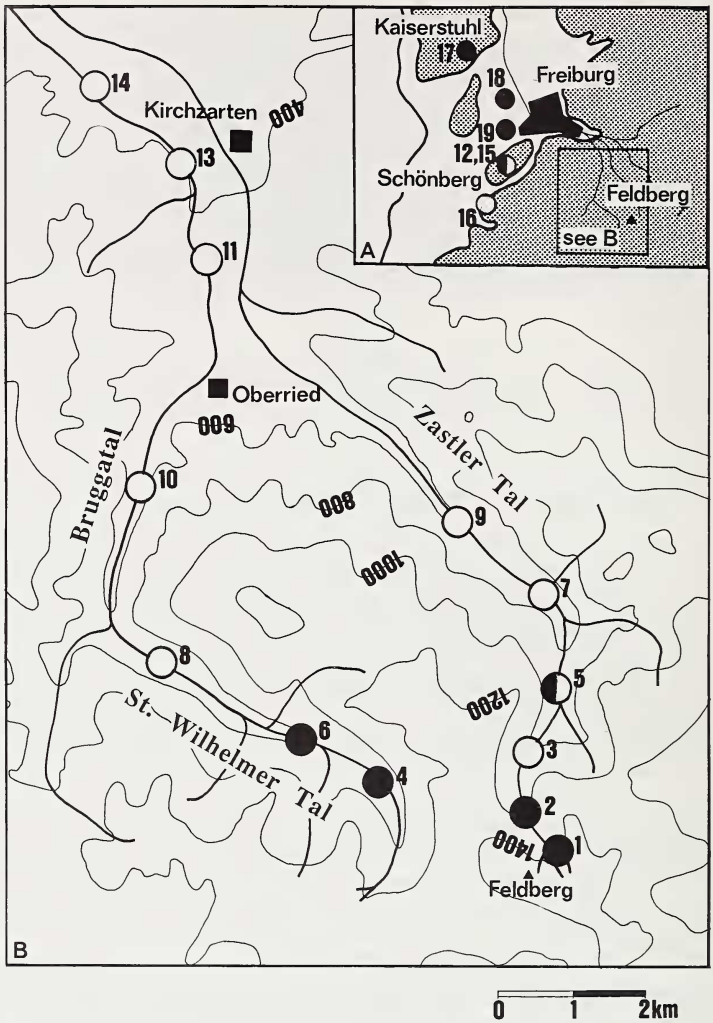

Fig. 1. Trapping sites and distribution of *S. araneus* (black circles) and *S. coronatus* (white circles) in the study area. The contact zone is given by a black and white circle. A: Freiburg region, in southwestern Germany, B: Feldberg region in the Black Forest. Locality numbers correspond to Table 1

coronatus and 3 of *S. araneus* were captured (Braun and Kischnick 1987). The shrews might have been taken from a contact zone but, at present, no additional data are available for this region.

Whereas the distribution of the *Sorex* species in the Black Forest corresponds to the situation throughout Europe described above, the occurrence of *S. araneus* in the Upper Rhine Valley, where it has already been found in Alsace by Hausser (1978), and the simultaneous absence of *S. coronatus* reveal a possible significance of drought and heat factors of the continental climate for the distributional ecology of the two species. An additional indication comes from the Catalan parts of the Pyrénées where the climate is dry, warm and Mediterranean-like and where *S. araneus* descends to low altitudes, while *S.*

coronatus is only found at 800–1500 m, although it is widespread in the Atlantic climate of northwestern Spain (Lopez-Fuster et al. 1985).

Ecological comparison of the two species

In contrast to *S. coronatus* having a relatively limited distribution in western Europe, *S. araneus* has a large distributional range from the Pyrénées to Lake Baikal in Siberia with its distributional centre in the continental east. As a species, *S. araneus* reveals greater ecological valency (Hausser and Bourquin 1988). This point is supported by some aspects of the evolutionary biogeography of the two shrew species. The British mainland, for example, with typical Atlantic climate, is only inhabited by *S. araneus* since *S. coronatus* did not arrive before its separation from the continent after the last glaciations. This species also did not succeed in passing the Alps to northern Italy. In these two regions *S. araneus* occupies all suitable habitats in the plains and in the mountain areas. As shown by Hausser and Bourquin (1988), in Switzerland *S. araneus* would be able to exist in most biotopes of the country. Its absence in the lowlands can more convincingly be explained by competition pressure going out from *S. coronatus* than by autoecological constraints (Neet and Hausser 1990). It should, however, be pointed out that *S. araneus* is not a simple species, but consists of several chromosomal types (e.g. Searle 1984; Hausser et al. 1985; Hausser et al. 1986; Reumer and Meylan 1986). To what extent are these races differentiated from an ecological point of view is not yet known and, obviously, this point may be of crucial importance in explaining the apparently wide ecological valency of *S. araneus*.

The principle stating that ecologically identical species cannot coexist (Gause 1934) is now widely accepted (Begon et al. 1986). As a consequence of the general similarity of *S. araneus* and *S. coronatus*, competition is an important factor in the lack of overlap of their distributional ranges (Hausser 1978; Neet and Hausser 1990). An ecological field analysis in Switzerland revealed that in two contact zones, the two species coexisted over a

Table 1. **List of trapping sites in southwestern Germany, classified by their altitudes**

Altitude (m a.s.l.)	Species	n (ind.) *S. araneus*/ *S. coronatus*	No.	Locality
1450	●	1/0	1	Feldberg, near top
1230	●	1/0	2	Feldberg, Zastler Hut
1050	○	0/1	3	Upper Zastler Valley
900	●	2/0	4	Upper St. Wilhelmer Valley
900	◐	3/3	5	Middle Zastler Valley
790	●	2/0	6	Upper St. Wilhelmer Valley
730	○	0/1	7	Lower Zastler Valley
700	○	0/7	8	Middle St. Wilhelmer Valley
600	○	0/1	9	Lower Zastler Valley
540	○	0/5	10	Bruggatal, near Oberried
420	○	0/2	11	Zartener Becken, near Oberried
400	◐	1/1	12	Schönberg, near Ebringen
390	○	0/1	13	Zartener Becken, near Kirchzarten
360	○	0/2	14	Zartener Becken, near Freiburg
350	○	0/1	15	Schönberg, near Ebringen
300	○	0/3	16	Border of Black Forest, near Ehrenkirchen
270	●	3/0	17	Kaiserstuhl, Liliental
230	●	4/0	18	Mooswald, northwest of Freiburg
215	●	42/0	19	Mooswald, southwest of Freiburg

Black circles = *S. araneus*, white circles = *S. coronatus*, black and white circle = contact zone. Locality numbers correspond to Fig. 1

limited zone of overlap by selecting different microhabitats, those of *S. araneus* having a thicker litter layer and higher soil humidity (Neet and Hausser 1990). It was also shown that *S. araneus* and *S. coronatus* occupy the same trophic niche in their zones of contact (Neet 1989a) and that equal intensities of intra- and interspecific competition for food as a limiting factor lead to interspecific territoriality (Neet 1989b). In other words, the two species do differ in terms of their ecoclimatic adaptations but are still too similar to coexist. This example thus illustrates the usefulness of the principle of limiting similarity proposed by Mac Arthur and Levins (1967).

If the high ecological similarity of *S. araneus* and *S. coronatus* does not allow sympatrical distribution, and although the contact zones we observe today seem to be relatively stabilized, one may suppose that, on an evolutionary time scale, one species will dominate the other and, with climatic changes, will replace it over an appreciable geographical space. This is how the distributional ecology of *S. araneus* and *S. coronatus* has been interpreted, since the actual distribution of the two species bears several indications that *S. coronatus* has forced *S. araneus* up to the north and east of Europe since the last glaciations. Moreover, the limited adaptations of both species to regionally or locally different climates in connection with mutual exclusion are considered to be characteristics of an early stage of ecological differentiation (Hausser 1984; Hausser et al. 1985).

The results presented here confirm the parapatric interpretation (e.g. Hausser et al. 1985; Hausser and Bourquin 1988) especially since there is a clear similarity between the situation in southwestern Germany and that in western Switzerland (Table 2). In central and northern Germany, the situation is less clear and the distribution is more mosaic-like. In that area, the distribution of the two species is sometimes considered as sympatrical (Hutterer pers. comm.). Handwerk (1987) reported ratios of *S. araneus*: *S. coronatus* of 1:1 to 1:3 for the plains of the Niederrhein and the Cologne–Bonn region, and 2:1 ratios

Table 2. **Comparison of the distributional ecology of *S. araneus* and *S. coronatus* in southwestern Germany and western Switzerland**

Data for western Switzerland are taken from Neet 1989a

	Southwestern Germany	Western Switzerland
Altitude range		
S. araneus	215–1450 m	380–1950 m
S. coronatus	300–1050 m	490–1340 m
Type of distribution	parapatric	parapatric
Relative habitat preferences		
S. araneus	cold (continental)	wet and cold
S. coronatus	warm (Atlantic)	dry and warm
	balanced humidity	
Breadth of contact zones	200–2000 m[a]	100–1000 m[b]
Ecological relationship in the contact zones		Habitat selection in response to interspecific competition Interspecific territoriality

[a] The breadth of the contact zones was estimated as follows: in the Zastler Valley, the breadth was estimated to be equivalent to the length of the trapping area, i. e. 200 m; in the St. Wilhelmer Valley the maximal breadth was estimated to be of 2000 m, which corresponds to the distance between capture points 6 and 8 (Fig. 1). – [b] Neet (1989a) indicates breadths around 100 m. However, in patchy areas (woodlands alternating with grasslands) it is difficult to estimate a precise value (see Neet and Hausser 1990). However, maximal values around 1000 m have been estimated.

for the adjacent regions of medium altitude. Neet and Hausser (1990) consider that the work of Handwerk (1987) lacks sufficient detail to ascertain whether the two species are sympatrically or parapatrically distributed in that area. A detailed ecological study might reveal local differentiation, which may be very subtle, as in the Swiss contact zones. Nevertheless, an alternative hypotheses exists and is due to the simple fact that resource availability influences interspecific competition. In the contact zones studied by Neet and Hausser (1990), there is evidence that food was a limiting factor (Neet 1989a) and that competitive pressure induced interspecific territoriality (Neet 1989b). If there are no limiting ressources, the situation may change. An example is given in the work by Llewellyn and Jenkins (1987) on the cricetids *Peromyscus maniculatus* and *P. truei*, where it was shown that there are seasonal changes in overlap of microhabitat niche, and that these changes may be explained by the degree of resource scarcity. In one of the contact zones studied in Switzerland, it was shown that the competitive pressure between *S. araneus* and *S. coronatus* is present throughout the year (Neet and Hausser 1990). However, the situation may be different in central and northern Germany. A seasonal variation in competitive pressures is a realistic hypothesis and may result in variations of the degree of overlap between the two species and limited sympatry.

Acknowledgements

One of us (H. B.) gratefully received important impulse for this work from Prof. G. Osche, University of Freiburg. We both thank Prof. P. Vogel and Prof. J. Hausser from the University of Lausanne for their support, interest and help in this research. The electrophoretic determinations were started in the Institute of Zoology and Animal Ecology of the University of Lausanne and later performed in the laboratory of Prof. H. Gutzeit, University of Freiburg, with friendly support of V. Grau. Traps were placed at disposal by M. Brau, Staatliches Museum für Naturkunde, Karlsruhe. The work was supported by Prof. Friedrich Kiefer-Fonds, Badischer Landesverein für Naturkunde und Naturschutz e. V. Many thanks are due to H. Brack for her invaluable help in the field.

Zusammenfassung

Eine parapatrische Szenerie: Die Verbreitung und Ökologie von Sorex araneus und Sorex coronatus (Insectivora, Soricidae) in Südwestdeutschland

Die Verbreitung von *Sorex araneus* und *Sorex coronatus* in Südwestdeutschland wurde in einem Transekt vom Oberrheingraben zum Feldberg im Schwarzwald untersucht. Die Artbestimmung geschah mittels einer Polyacrylamid-Gelelektrophorese des Gesamtbluteiweißes. Im Untersuchungsraum waren die beiden Arten parapatrisch verbreitet, und dies in Form einer alternierenden Höhenverbreitung. *S. araneus* wurde im Oberrheintal und am oberen Feldberg angetroffen, *S. coronatus* in den unteren und mittleren Schwarzwaldlagen. Im klimatisch begünstigten Zastler Tal reicht die Verbreitung von *S. coronatus* 400 Höhenmeter weiter talaufwärts als im kälteren und rauheren St. Wilhelmer Tal. Zwei Kontaktzonen, eine obere und eine untere, wurden ausfindig gemacht. Im Untersuchungsgebiet können die beiden Arten als höhenvikariierende Arten bezeichnet werden. Die Ökologie und Verbreitungsgeschichte von *S. araneus* und *S. coronatus* wird anhand der bisher bekannt gewordenen Daten über ihre Lebensräume diskutiert. *S. araneus* besiedelt Gebiete mit eher kontinentalem Charakter sowie Lebensräume mit nassen und trockenen Böden. Dagegen bevorzugt *S. coronatus* atlantisches Klima und ausgeglichene Bodenfeuchtigkeit.

References

Baker, R. J.; Haiduk, M. W.; Robbins, L. W.; Cadena, A.; Koop, B. F. (1982): Chromosomal studies of South American bats and their systematic implications. Special publ. Pymatuning Lab. Ecol. **6**, 303–327.

Begon, M.; Harper, J. L.; Townsend, C. R. (1986): Ecology. Individuals, Populations and Communities. Oxford: Blackwell.

Braun, M.; Kischnick, P. (1987): Spitzmäuse und ihre Nahrung in einem Buchenwald. Carolinea **45**, 159–160,

Brünner, H.; Hoffrichter, O. (1987): Neue Fundorte der Alpenspitzmaus (*Sorex alpinus* Schinz, 1837) im Südschwarzwald. Mitt. bad. Landesver. Naturkunde u. Naturschutz N.F. **14**, 403–408.

Gause, G. F. (1934): The struggle for existence. Baltimore: Wiliams and Wilkins Co.: (1934). New York: Hafner Publ. (Repr. 1964).

Handwerk, J. (1987): Neue Daten zur Morphologie, Verbreitung und Ökologie der Spitzmäuse *Sorex araneus* und *S. coronatus* im Rheinland. Bonn. zool. Beitr. **38**, 273–297.

Hausser, J. (1978): Répartition en Suisse et en France de *Sorex araneus* L., 1758 et de *Sorex coronatus* Millet, 1828 (Mammalia, Insectivora). Mammalia **42**, 329–341.

— (1984): Genetic drift and selection: Their respective weights in the morphological and genetic differentiation of four species of shrews in Southern Europe (Insectivora, Soricidae). Z. zool. Syst. Evolut.-forsch. **22**, 302–320.

— (1990): *Sorex coronatus* Millet, 1828. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer and F. Krapp. Wiesbaden: Aula-Verlag.

Hausser, J.; Bourquin, J.-D. (1988): Répartition de douze espèces de mammifères en Suisse. Atlas des Mammifères de Suisse. Société suisse pour l'étude de la faune sauvage, Lausanne.

Hausser, J.; Catzeflis, F.; Meylan, A.; Vogel, P. (1985): Speciation in the *Sorex araneus* complex (Mammalia: Insectivora). Acta Zool. Fennica **170**, 125–130.

Hausser, J.; Dannelid, E.; Catzeflis, F. (1986): Distribution of two karyotypic races of *Sorex araneus* (Insectivora, Soricidae) in Switzerland and the post-glacial recolonization of the Valais: First results. Z. zool. Syst. Evolut.-forsch. **24**, 307–314.

Hausser, J.; Hutterer, R.; Vogel, P. (1990): *Sorex araneus* L. 1758. In: Handbuch der Säugetiere Europas. Ed. by J. Niethammer and F. Krapp. Wiesbaden: Aula-Verlag.

Hausser, J.; Zuber, N. (1983): Détermination spécifique d'individus vivants des deux espèces jumelles *Sorex araneus* et *S. coronatus*, par deux techniques biochimiques (Insectivora, Soricidae). Rev. suisse Zool. **90**, 857–862.

Hutterer, R.; Vierhaus, H. (1984): Waldspitzmaus, Schabrackenspitzmaus. In: Die Säugetiere Westfalens. Ed. by R. Schröpfer; R. Feldmann and H. Vierhaus. Münster: Abh. Westf. Mus. Naturkunde **4**, 54–60.

Knoch, D. (1989): Säugetiere im Belchengebiet. In: Der Belchen im Schwarzwald. Die Natur- und Landschaftsschutzgebiete Baden-Württembergs 13. Landesanstalt für Umweltschutz, Baden-Württemberg, 1159–1165.

Liehl, E.; Sick, W. D. (1984): Der Schwarzwald – Beiträge zur Landeskunde. 3 ed. Ver. Allemann. Inst. Freiburg i. Br. 47. Bühl, Baden: Konkordia.

Llewellyn, J. B.; Jenkins, S. H. (1987): Patterns of niche shift in mice: Seasonal changes in microhabitat breadth and overlap. Am. Nat. **129**, 365–381.

Loch, R. (1977). A biometrical study of karyotypes A and B of *Sorex araneus* Linnaeus, 1758, in the Netherlands (Mammalia, Insectivora). Lutra 19, 21–36.

Lopez-Fuster, M. J.; Gosalbez, J.; Sans-Coma, V. (1985): Presencia y distribucion de *Sorex coronatus* Millet, 1828 (Insectivora, Mammalia) en el NE ibérico. P. Dept. Zool. Barcelona 11, 93–97.

Mac Arthur, R. H.; Levins, R. (1967): The limiting similarity, convergence and divergence of coexisting species. Am. Nat. 101, 377–385.

Meylan, A. (1964): Le polymorphisme chromosomique de *Sorex araneus* L. (Mammalia, Insectivora). Rev. suisse Zool. **71**, 903–983.

Meylan, A.; Hausser, J. (1978): Le type chromosomique A des *Sorex* du groupe *araneus: Sorex coronatus* Millet, 1828 (Mammalia, Insectivora). Mammalia **42**, 115–122.

Mys, B.; van der Straeten, E.; Verheyen, W. (1985): The biometrical and morphological identification and the distribution of *Sorex araneus* L., 1758 and *S. coronatus* Millet, 1828 in Belgium (Insectivora, Soricidae). Lutra **28**, 55–70.

Neet, C. R. (1989a): Ecologie comparée et biogéographie évolutive de deux espèces parapatriques: *Sorex araneus* et *S. coronatus* (Mammalia, Insectivora, Soricidae). Ph. D. thesis, University of Lausanne.

— (1989b): Evaluation de la territorialité interspécifique entre *Sorex araneus* et *S. coronatus* dans une zone de syntopie (Insectivora, Soricidae). Mammalia **53**, 329–335.

Neet, C. R.; Hausser, J. (1989): Chromosomal rearrangements, speciation and reproductive isolation: the example of two karyotypic species of the genus *Sorex*. J. evol. Biol. **2**, 373–378.

— — (1990): Habitat selection in zones of parapatric contact between the common shrew *Sorex araneus* and Millet's shrew *S. coronatus*. J. Anim. Ecol. **59**, 235–250.

Olert, J. (1973): Cytologisch-morphologische Untersuchungen an der Waldspitzmaus (*Sorex araneus* Linne, 1758) und der Schabrackenspitzmaus (*Sorex gemellus* Ott, 1968. (Mammalia – Insectivora). Veröffentl. Univ. Innsbruck **76**, 1–73.

Ott, J. (1968): Nachweis natürlicher reproduktiver Isolation zwischen *Sorex gemellus* sp. n. und *Sorex araneus* Linnaeus, 1758 in der Schweiz (Mammalia, Insectivora). Rev. suisse Zool. **75**, 53–75.

Reumer, J. W. F.; Meylan, A. (1986): New developments in vertebrate cytotaxonomy IX: Chromosome numbers in the order Insectivora (Mammalia). Genetica **70**, 119–151.
Schwammberger, K. H. (1976): Nachweis der Schabrackenspitzmaus (*Sorex gemellus* Ott, 1968) in Westfalen. Natur u. Heimat **36**, 66–69.
Seabright, M. (1971): A rapid banding technique for human chromosomes. Lancet **2**, 971–972.
Searle, J. B. (1984): Three new karyotypic races of the common shrew *Sorex araneus* (Mammalia: Insectivora) and a phylogeny. Syst. Zool. **33**, 184–194.

Authors' addresses: Harald Brünner, Institut für Biologie I (Zoologie), Albertstraße 21a, Albert-Ludwigs-Universität, W-7800 Freiburg/Br., FRG, and Dr Cornelis R. Neet, Conservation de la faune, Chemin du Marquisat 1, CH-1025 St. Sulpice, Switzerland